A NEW EUTELEOSTEAN FISH FROM THE LOWER CRETACEOUS OF TUCANO BASIN, NORTH-EASTERN BRAZIL [1]

(With 8 figures)

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ABSTRACT: A new euteleostean fish, *Britoichthys marizalensis* gen. and sp.nov. is described from the Lower Cretaceous of Tucano basin, North-eastern Brazil, based on various almost complete and articulate specimens preserved in a yellowish siltstone yielded from Marizal Formation. This taxon is recognised by an unique combination of characters: an ethmoidean commissure on rostrodermethmoid bone; well-developed premaxilla with fang-like teeth; presence of a sinuous maxilla with oral border garnished of aligned conical teeth; massive mandible with straight oral border; reduced orbit bordered by large infraorbital bones; seven branchiostegals rays; three uroneurals, the first not extending forward beyond the preural centrum 1; ural centra not fused; membranous outgrowth (stegural) of first uroneural; leaf-like plates of bone associated with rudimentary neural arches of the first preural and ural vertebrae; non bifurcate epineurals, pattern 2 supraneurals, cycloid scales, and 36 vertebrae. The reduced number of vertebrae and branchiostegal rays, premaxilla shape, caudal endoskeleton pattern, simple epineurals, supraneural type, and the presence of a retroarticular in the corner of the lower jaw suggest affinities with euteleostean fishes. In so far as known, *Britoichthys* is unique in its combination of features and cannot be included in any known family.

Key-words: *Britoichthys marizalensis* gen. and sp.nov., Euteleostei, Lower Cretaceous, Tucano Basin.

RESUMO: Um novo peixe euteleósteo do Cretáceo Inferior da Bacia do Tucano, Nordeste do Brasil.

Um novo peixe euteleósteo, *Britoichthys marizalensis* gen. e sp.nov., é descrito do Cretáceo Inferior da Bacia do Tucano, Nordeste do Brasil, com base em espécimes praticamente completos e articulados preservados em um siltito amarelado produzido na Formação Marizal. Esse táxon é reconhecido por uma combinação única de caracteres: comissura etmoideana no rostrodermetmóide; pré-maxilar bem desenvolvido e com dentes agudos; presença de um maxilar sinuoso provido de dentes cônicos alinhados; mandíbula bem ossificada e com bordo oral reto; órbita reduzida e margeada de grandes ossos infraorbitais; sete raios branquiostégios; três uroneurais, o primeiro não se estendendo adiante além do primeiro centro preural; centros urais não fusionados; projeção membranosa (estegural) do primeiro uroneural; lâminas ósseas em forma de folha associadas com arcos neurais rudimentares dos primeiros centros pré-ural e ural; epineurais simples (não bifurcados); padrão tipo 2 de supraneurais; escamas ciclóides; e trinta e seis vértebras. O reduzido número de vértebras e raios branquiostégios, o formato do pré-maxilar, o padrão do endoesqueleto caudal, epineurais simples, o padrão de supraneural, e a presença de um retroarticular no canto da maxila inferior sugerem afinidades com peixes euteleósteos. Até onde se sabe, *Britoichthys* é único em sua combinação de caracteres e não pode ser incluído em qualquer família conhecida.

Palavras-chave: *Britoichthys marizalensis* gen. e sp.nov., Euteleostei, Cretáceo Inferior, Bacia do Tucano.

INTRODUCTION

The scientific knowledge about fishes from the Marizal Formation began with a series of studies done by the late paleontologist Rubens da Silva Santos (1918-1996). He pointed out the presence of Amiidae, Clupavidae, Macrosemiidae, Cladocyclidae, Chanidae, and Aspidorhynchidae for that stratigraphic unit (SANTOS, 1972, 1973, 1976,

1985 and 1990). Some fishes were described as new species. He assigned an Aptian age for the strata based on the occurrence of the chanid *Dastilbe elongatus* Santos, 1947, attempting for similarities on the taxonomic composition among Marizal, Marfim, and Muribeca formations. Taking into account that *Dastilbe elongatus* is also found in association with plants, insects, shrimps and ostracods at the Crato Member, from the Chapada

do Araripe, he claimed a probable estuarine environment (SANTOS, 1972).

According to SANTOS (1972), taxa described from the Marizal Formation demonstrate having spatial and temporal correlation with certain fish species described from the Cretaceous of Gabon (see ARAMBOURG & SCHNEEGANS, 1935). Despite this, no detailed study dealing with systematics and biogeography of these species has been realised in order to evaluate his hypothesis critically.

Beyond the contributions of Silva Santos dealing with Marizal´s fishes, some sparse descriptions and new records of taxa have been made (TAVERNE, 1977; BRITO, 1997; ALCÂNTARA & FIGUEIREDO, 1999, 2000). In this context, the present paper describes a new teleost taxon, *Britoichthys marizalensis* gen. and sp.nov., by far the most abundant fish from the Marizal Formation at the Cicero Dantas locality, North-eastern Bahia. In addition, a discussion of its systematic position is presented.

GEOLOGICAL SETTING

The basins belonging to the Recôncavo-Tucano-Jatobá trend extends over an area of more than 46,500 square kilometers North-eastern Bahia State, septentrional Brazil. The Tucano basin, where the Marizal Formation is widely spread, stretches from the Irará-Ouriçangas region northwards, reaching the São Francisco river. This formation covers about 2/3 of the Recôncavo-Tucano-Jatobá basins, with a thickness of about 150m reaching 300m in the vicinities of Cícero Dantas, at the Central Tucano (BRITO, 1979). By contrast, it is less represented in the Recôncavo and Jatobá basins (SANTOS, 1972).

According to BRAZIL (1947) the Marizal Formation is defined on the basis of certain sandstones, conglomerate beds, clastics and some limestones above the Bahia Group. Revised studies of the Marizal Formation (VIANA *et al.*, 1971) divided it into three members: a lower one, composed of fine clastics, sandstones and conglomerates of quartzite and gneiss; an intermediary, including mainly shales, siltstones and fine sandstones, with slender layers of limestone; and an upper member composed of siltstones and sandstones, and rarely gypsum.

Some authors (BRAUN, 1966; MAISEY, 2000), agreeing with SANTOS (1972), pointed out a correlation of Marizal Formation with part of Muribeca Formation of the Sergipe-Alagoas Basin based on geological and paleontological data.

Most common fossils in the assemblage of Marizal Formation are plants (BARBOSA, 1950), decapod shrimps (ROXO, 1940; BEURLEN, 1950), ostracods and palynomorphs (BRITO, 1979; ARAI, HASHIMOTO & UESUGUI, 1989), and fishes.

MATERIAL AND METHODS

The taxon herein described is based on various nearly complete articulated specimens of small size. Because no incomplete ossification of bones is observed on the skeletons, it is assumed that the specimens are all adults.

The fossil fish material belongs to the paleontological collections of the Departamento Nacional de Produção Mineral and Universidade do Estado do Rio de Janeiro, and is referred in this paper by the institutional abbreviations DGM and Pz.DBAV.UERJ respectively, followed by the register number. Most of material was obtained in Cícero Dantas by the geologist José Lino de Melo Junior in the late 1930's and Rubens da Silva Santos in the 1940's (SANTOS, 1990).

All fossils are preserved in a yellowish siltstone. Most of the bones are represented in the matrix by a slight reddish imprint and some specimens show slightly a crushed or broken skeleton. Occasionally, there are distorted specimens in the same bedding planes suggesting a probable lentic taphonomic environment. In addition, various specimens are complete and articulated, suggesting few or null action of scavengers.

Ethyl acetate was dropped on the surface of the fossils to enhance skeletal structures. The drawings of specimens were made using Nikon SMZ 800 stereomicroscope with camera lucida attachment.

Anatomical abbreviations – (r) and (l) are used before anatomical terms indicating right and left side, respectively: (AA) anguloarticular; (alv.p.) alveolar process of premaxilla; (ACH) anterior ceratohyal; (a.fo.) anterior fontanel; (ANT) antorbital; (ar.pr.PMX) articular process of premaxilla; (a.pr.PMX) ascending process of premaxilla; (ASPH) autosphenotic; (BRR) branchiostegal rays; (CL) cleithrum, (CO) coracoid; (CPU) preural centrum; (D) dentary; (DSPH) dermosphenotic; (ECPT) ectopterygoid; (ENPT) endopterygoid; (EP) epural; (EPN) epineural; (EPO) epioccipital; (ep.c.) epiphyseal sensory canal; (ethm.c.) ethmoideal commissure; (EXS) extrascapular; (FR) frontal; (f.r.) fin ray; (H) hypural; (HD) dorsal hypohyal; (HM) hyomandibula; (HV) ventral hypohyal; (h.sp.)

hemal spine; (IO) infraorbital; (io.c.) infraorbital canal; (IOP) interoperculum; (LA) lachrymal; (LET) lateral ethmoid; (md.c.) mandibular canal; (MPT) metapterygoid; (MX) maxilla; (NA) nasal; (n.a.) neural arch; (NS) neural spine; (OP) operculum; (op.pr.HM) opercular process of hyomandibula; (PA) parietal, (pa.c.) parietal canal; (PAS) parasphenoid; (PCH) posterior ceratohyal; (PCL) postcleithrum; (p.fo.) posterior fontanel; (PH) parhypural; (PMX) premaxilla; (POP) preoperculum; (pop.c.) preopercular canal; (PTM) post-temporal; (PTO) pterotic; (PU) preural centrum; (Q) quadrate; (rad) radial; (RAR) retroarticular; (RBR) branchiostegal rays; (rad) radial bone; (RETM) rostrodermethmoid; (S) sympletic; (SCL) supracleithrum; (scl.b.) sclerotic bone; (SMX) supramaxilla; (SN) supraneural; (SCA) scapula; (SCL) supracleithrum; (SOC) supraoccipital; (SOP) suboperculum; (SORB) supraorbital; (sorb.c.) supraorbital sensory canal; (ST) stegural; (t) teeth; (U) ural centrum; (UN) uroneural; (V) vertebra.

SYSTEMATIC PALEONTOLOGY

TELEOSTEI Müller, 1844

CLUPEOCEPHALA Patterson & Rosen, 1977

EUTELEOSTEI Greenwood *et al.*, 1967

Family indeterminate

Britoichthys gen.nov.

Type (and only) species – *Britoichthys marizalensis* sp.nov.

Etymology – In honour of the late geologist Ignácio Aureliano Machado Brito (1938-2001) for remarkable contributions for the Brazilian paleontology; plus the Greek word, *ichthys*, a fish.

Diagnosis – A small and elongated fish reaching about 100mm in total length exhibiting the following combination of features: head length contained four times within the total length; small orbit bordered with large circumorbital plates; maximum body depth contained seven times within the total length; dermal skull bones smooth; ethmoideal commissure on a sagitate rostrodermoethmoid bone; supraorbital sensory canal lying superficially enclosed in bony tube and showing tripartite pattern posteriorly; parietal bones in contact medially; two fontanels on the

skull roof; long supraorbital bone; sinuous maxilla with oral border garnished with aligned series of conical teeth; fang-like dentition on the oral border of a premaxilla; premaxilla with well-developed ascending and articular processes and produced alveolar process under maxilla; two supramaxillaries; massive lower jaw with high coronoid process; dentary deep with oral border straight; retroarticular excluded from the articular surface; parasphenoid, endopterygoid and ectopterygoid toothless; vertical branch of preoperculum slightly larger than the horizontal branch and with accentuate convex ventral border; very reduced tubules of preopercular sensory canal; long and drop-like post-temporal; homocercal caudal fin deeply forked; six hypurals; three uroneurals, the first non extending forward after first preural centrum; ural centra autogenous; two epurals; membranous outgrowth (stegural) on first uroneural; leaf-like plate of bone associated with rudimentary neural arch on first preural and ural centra; overlapping cycloid scales with marked concentric circuli not extending onto skull or fins; pattern 2 supraneural; simple epineural ribs; seven branchiostegals rays and 36 vertebrae.

Britoichthys marizalensis, sp.nov.
(Figs.1-8)

Etymology – After Marizal Formation where the fish fossil was yielded.

Diagnosis – as for the genus (by monotypy).

Holotype – DGM 466-P, a well preserved and complete fish.

Referred material – DGM 465, anterior half of fish showing suspensorium and mandibles; DGM 467, mandible; DGM 536, almost complete fish lacking most of skull; DGM 539, nearly complete fish wanting caudal fin rays; DGM 540, nearly complete fish; DGM 541, fish lacking part of skull and tail; DGM 542, nearly complete fish lacking rays of caudal fin; DGM 543, fish lacking tail; DGM 1024, fish lacking tail; DGM 1027, skull and part of trunk; Pz.DBAV.UERJ 414, complete and twisted fish; Pz.DBAV-UERJ 415, skull roof.

Meristic data – 36 vertebrae (18 abdominal); D i,12; P 15 -16; V 10; A i,10; C x, I, 9, 8, I, ?vi.

Stratigraphy – Siltstones from the Marizal Formation outcropping at the locality of Quatis farm, highway Cícero Dantas-Jeremoabo (BR110), city of Cícero Dantas (10°35'30"S 38°21'40"W), State of Bahia (see SANTOS, 1972, 1990). The

Aptian age is sustained by ARAI, HASHIMOTO & UESUGUI (1989) and CAIXETA *et al.* (1994).

Paleoecology – *Britoichthys marizalensis* gen. *et* sp.nov. was a probable shoaling fish since various individuals are frequently occurring on the same bedding plane. It is probably associated with shrimp assemblage since in some individuals there are faint imprints of shrimps in the region corresponding to the digestive tract.

ANATOMICAL DESCRIPTION

Britoichthys marizalensis gen. and sp.nov. is an elongated fish with a relatively large head (roughly *Esox*-shaped) whose maximum depth is of about 2/3 head length (Fig.1). The bones of the dermocranium are mainly flat and smooth, devoid of ornamentation. The sensory canals when present are totally enclosed in dilated bony tubes. The body may have been laterally compressed, since all the specimens are preserved in lateral view. The mouth is large and terminal and the orbit is relatively short. The dorsal fin is deep with a short base and it is placed at the midpoint of the back. The pelvic fin is located slightly behind the origin of the dorsal fin. The origin of the short anal fin is in the midpoint between pelvic and caudal fins. The caudal fin is homocercal forked type. A tentative reconstruction of the fish based mainly on the holotype is shown (Fig.2) and measures of most complete and well-preserved specimens are shown in the table1.
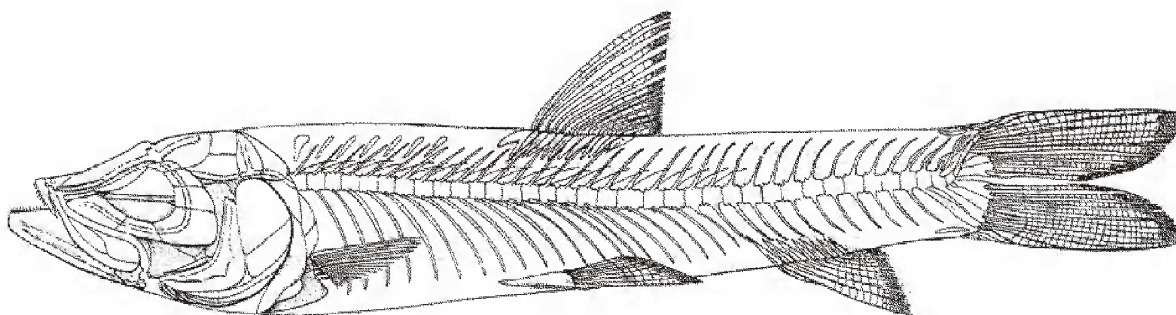
Britoichthys marizalensis gen. and sp.nov.: fig.1- holotype DGM 466-P (scale bar = 0.5cm); fig.2- restoration of whole skeleton, scales omitted.

Table 1. Measurements in milimetres of specimens of *Britoichthys marizalensis* gen. and sp.nov.

NUMBER DGM	TOTAL LENGTH	STANDARD LENGTH	HEAD LENGTH	TRUNC DEPTH	PREDORSAL LENGTH	PREPELVIC LENGTH	PREANAL LENGTH
466	36.69	29.53	8.99	4.66	16.14	16.47	24.97
536	*100.00	*74.00	*24.00	15.41	*40.00	*43.50	*62.00
539	*48.50	42.47	12.54	8.77	20.13	23.60	32.42
540	42.16	33.31	10.52	7.43	8.98	8.99	18.49
541	?	?	*11.00	8.56	*20.00	*22.50	*29.90
542	?	*36.90	*11.00	7.60	20.21	20.72	26.71
543	?	?	12.00	8.27	22.35	24.89	?

(*) indicates estimate measurement on incomplete specimen.

Britoichthys gen.nov. possesses a sagitate rostro dermoethmoid (Figs.3-5, RETM) showing a conspicuous transverse tubular dilation of ethmoideal commissure. There are minute pores associated with the commissure. From each side of the bone there is a very reduced and round lateral process. No isolate mesethmoid is visible.

The nasal (Figs.3-4, NA) is a slender and elongate bone partially lying on the anterior end of the frontal and partially on the lateral margin of rostrodermoethmoid behind the lateral process. The bone is mainly reduced to its neurodermal component.

The lateral ethmoid (Fig.4, LET) is typically placed at the anterior limit of the orbitotemporal region. It is slightly arched and reduced to a flimsy perichondral lamina not extending below the level of parasphenoid.

The frontal (Figs.3-5, FR) is the largest bone of the skull roof. It is narrow above the orbit and laterally expanded in the posterior third. The frontal meets the parietal posteriorly via an oblique contact zone. Posterolaterally, each bone meets the pterotic through a gently sinuous joint. There is a fusiform anterior fontanel (Fig.5, a.fo.) separating medially the anterior part of frontals and immediately behind the orbit region, there is an oval posterior fontanel (Fig.5, p.fo.).

The main supraorbital sensory canal (Fig.3, sorb.c.) runs centrally throughout a conspicuous bony tube on the surface of the bone. Above the posterior part of the orbit the canal runs towards the autosphenotic. It gives off two branches, one short and medial corresponding to the epiphyseal canal (Fig.3, ep.c.) and other corresponding to a long parietal canal (Figs.3, pa.c.) that does not reach the parietal bone. The parietal (Figs.3-5, PA) is a moderately trapezoidal bone that contacts its antimere medially. Pit-lines, commissures and sensory canal are lacking.

The autosphenotic (Fig.4, ASPH) is a short triangular bone placed on the posterodorsal corner of the orbit. It seems to contribute for a shallow dilatator fossa and a reduced oblique facet for anterior head of hyomandibula. Laterally, there is a short spine-like process for the attachment of the dermosphenotic bone.

The pterotic (Figs.3-5, PTO) is a roughly L-shaped bone in dorsal view. Anteriorly it is sutured to the autosphenotic. It meets the frontal anteromedially and the parietal postero-medially. The pterotic occupies the postero-lateral border of neurocranium, bearing a bony tube for the otic sensory canal close to its lateral margin. Posteriorly, the bone is prolonged in a short spine-like process. There is no evidence of a *recessus lateralis* or a temporal fenestra.

In DGM 542-P there is an imprint of orbitosphenoid (Fig.4, ORPH) showing a reduced anterior process and short opening to cranial cavity. Posteriorly, it is followed by an imprint of a short pterosphenoid (Fig.4, PTS) forming with it the posterior limit of orbit. From basisphenoid (Fig.4, BSPH) is visible only a faint imprint of a slender vertical lamina (belophragme) projecting forwards in the posteroventral corner of the orbit.

The parasphenoid (Figs.3-4, PAS) is visible as a straight shaft of bone below the orbit. It seems to be entirely toothless and finishes at the level of the lateral ethmoid. The ascending process appears to be reduced and blunt.

The circumorbital series is compound of a single supraorbital, a single antorbital and six thin and large infraorbital plates covering most of the cheek. The infraorbital sensory canal is totally enclosed in tubular dilation but no exit for sensory tubules on surface were observed.
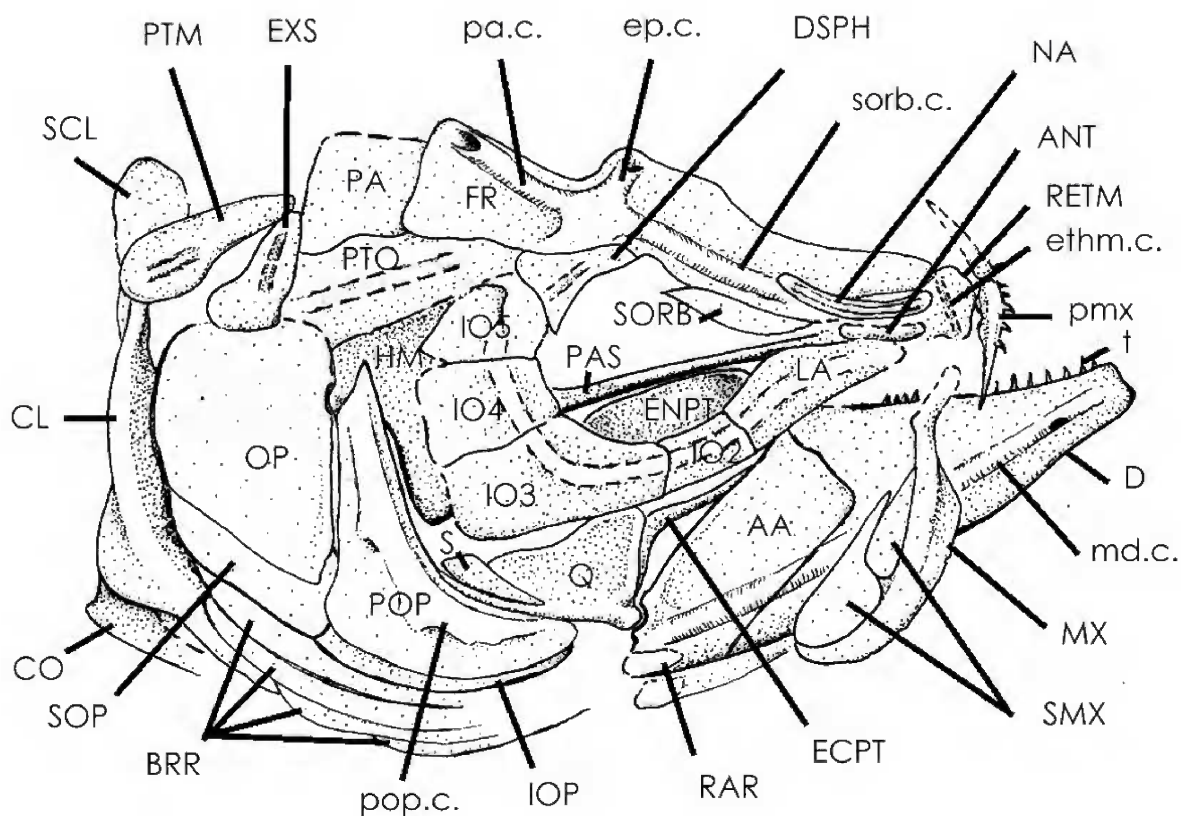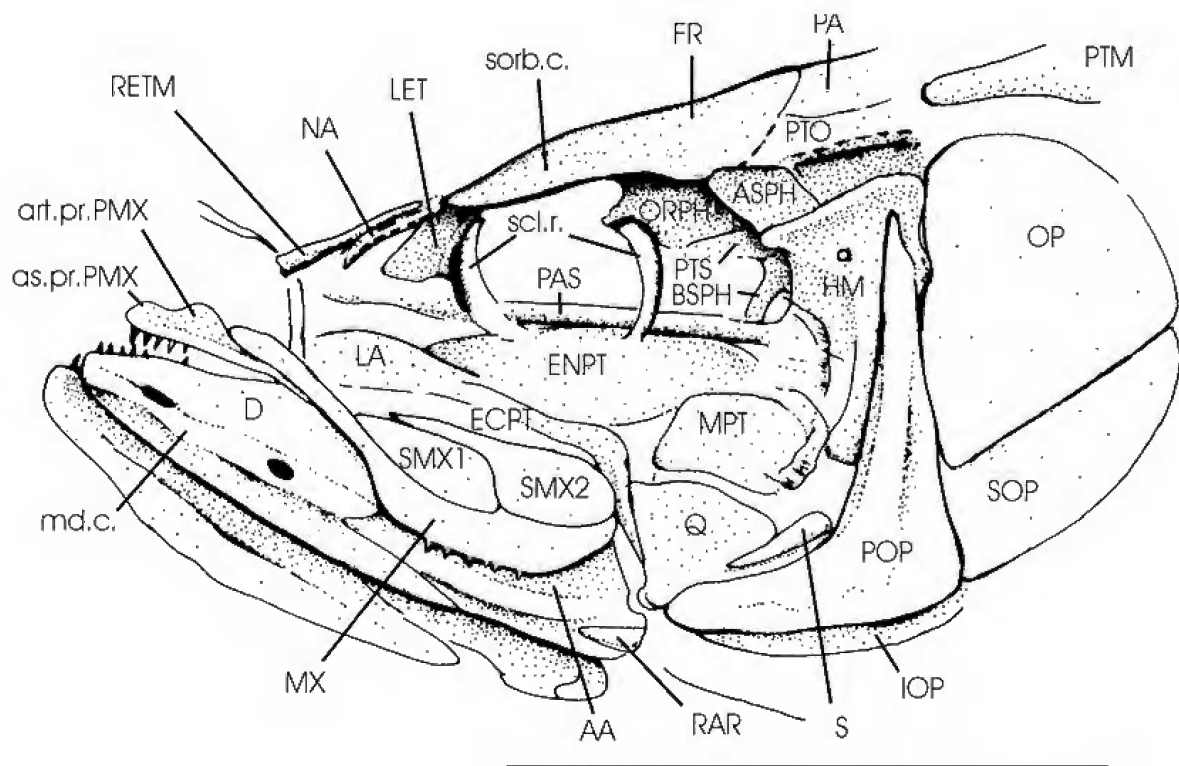
Britoichthys marizalensis gen. and sp.nov.: fig.3- skull as preserved in Pz.DBAV.UERJ 414, right lateral view; fig.4- skull as preserved in DGM 543-P, left lateral view. Scale bars = 0.5cm.
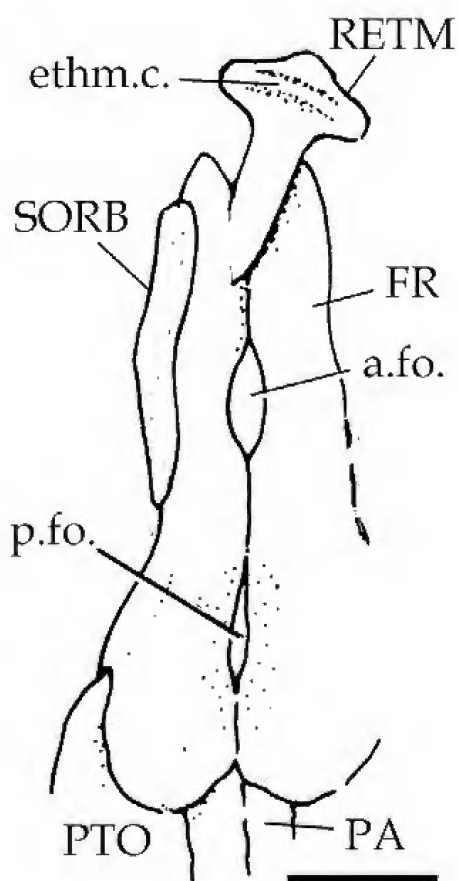
Fig.5- *Britoichthys marizalensis* gen. and sp.nov.: dorsal view of the cranial roof as preserved in the Pz.DBAV-UERJ 415. Scale bar = 0.25cm.

The supraorbital is a long and lanceolate anamestic bone obliquely located at the anterodorsal limit of orbitotemporal region (Figs.3, 5, SORB). It meets the anterior portion of frontal medially.

The lachrymal (Figs.3-4, LA) is a large trapezoidal bone. It is tightly jointed with the antorbital bone along its dorsal border. Posteriorly, it meets the shallow and subrectangular second infraorbital (Figs.3, IO 2). The third infraorbital bone (Figs.3, IO 3) is the largest of the set. It is trapezoid and partially covers the dorsal surface of quadrate and sympletic in the posteroventral corner of the cheek.

The fourth infraorbital (Fig.3, IO 4) is squarish and smaller than the third. It covers the region occupied by hyomandibula and metapterygoid. The fifth is slender and long (Fig.3, IO 5). The dermosphenotic (Fig.3, DSPH) is short and triangular. It covers the reduced *dilatator fossa* and bears a short bifurcation of infraorbital sensory canal.

The antorbital (Fig.3, ANT) is an arched club-shaped bone practically reduced to its neurodermal component. It forms the lateral border of the olfactory region.

Two separated and curved skeletal structures bordering the orbit in the DGM 542-P are interpreted as remains of the sclerotic ring (Fig.4, scl.r.).

The bones forming the oral border are well-preserved and garnished at most part of length of a single row of teeth. The premaxilla (Fig.3, PMX) is roughly triangular in lateral view. It shows rounded ascending (Fig.4, as.pr.PMX) and articular processes (Fig.4, art.pr.PMX). The alveolar process, bearing curved laniariform teeth, is relatively long and placed under maxilla as in *Ginsbourgia operta* (Patterson, 1970).

The maxilla (Figs.3-4, MX) is a large, sinuous and long bone. Its proximal portion is narrow finishing in a short articular head. Posteriorly, it is spatulate and arched covering a great part of lateral border of lower jaw, but not reaching the quadrate. The teeth are conical and spaced, and they are smaller than that of premaxilla.

There are two supramaxillae (Figs.3-4, 6, SMX). The anterior supramaxilla is a spindle-shaped bone whereas the posterior one is drop-shaped, showing a prominent anterior spine-like process overlapping the dorsal border of the first.

From lower jaw, dentary, anguloarticular and retroarticular bones were preserved. The dentary (Figs.3-4, 6, D) is a massive V-inverted shaped bone bearing a deep and long coronoid process. The symphysis region is low, smooth and without indentation. Large and curved caniniform teeth (Figs.3-4, t) are present along the oral border. A large mandibular sensory canal (Figs.3-4, md.c.) crosses the bone in a straight line longitudinally near ventral border. A reduced triangular retroarticular (Figs.3-4, RAR) is placed on the posterior corner of the lower jaw. The anguloarticular (Figs.3-4, 6, AA) is a massive triangular bone, with a well developed coronoid process. It possesses a wide articular surface for the quadrate bone. The mandibular sensory canal runs in a straight line along the ventral border of the bone.

From the hyobranchial apparatus only dorsal and ventral hypohyals, anterior and posterior ceratohyals, and some isolated faint imprints of branchial arches are visible. The dorsal and ventral hypohyals (Fig.6, DH and VH) are nodular bones of equal size. The anterior ceratohyal (Fig.6, ACH) is hour-glass shaped and elongate. A long, narrow, and arched groove for hyoidean artery crosses the bone near the dorsal margin. There are, at least, four long and falcate branchiostegal rays lodged externally on shallow foveae. The posterior ceratohyal (Fig.6, PCH) is a

triangular bone. It meets the anterior ceratohyal probably through a straight line of cartilage. There are three well developed and falcate branchiostegal rays with capitate proximal end (Figs.3, 6, BRR). The first two are more slender and the last is the thickest. They are also housed in shallow foveae on surface of the bone.

There is none evidence of gular plate. The quadrate (Figs.3-4, 6, Q) is a triangular bone with a slightly convex dorsal border. It bears a deep posterior notch on its posterior margin lodging a well-developed club-like sympletic (Figs.3-4, 6, S). The medial and lateral condyles of the quadrate are well-developed, slightly inclined forwards, and are located somewhat in front of the posterior end of orbit. The posteroventral process of the quadrate is slender and slightly arched. The hyomandibula (Figs.3-4, 6, HM) is a large and quadriform bone. Its ventral

process is reduced and the opercular process (Fig.6, op.pr.HM) is rounded and short. Anteriorly, hyomandibula produces a large laminate outgrowth meeting the endopterygoid and metapterygoid bones.

The ectopterygoid (Figs.3-4, 6, ECPT) is an edentulous boomerang-shaped bone meeting the quadrate posteriorly and the endopterygoid dorsally. It has a shallow lateral crest along its length. The metapterygoid (Figs.4, 6, MPT) is a small squarish bone located among the hyomandibula, quadrate, and endopterygoid. There is no evidence of fenestra with margins of these bones. The toothless endopterygoid (Figs.3-4, 6, ENPT) is a large elliptical bone. There are no teeth on its oral border. In front of the endopterygoid there is a short rod-like palatine (Fig.6, PAL).

The preoperculum (Figs.3-4, 6, POP) is L-shaped. The vertical and horizontal arms are approximately equal. The ventral border of this bone is moderately
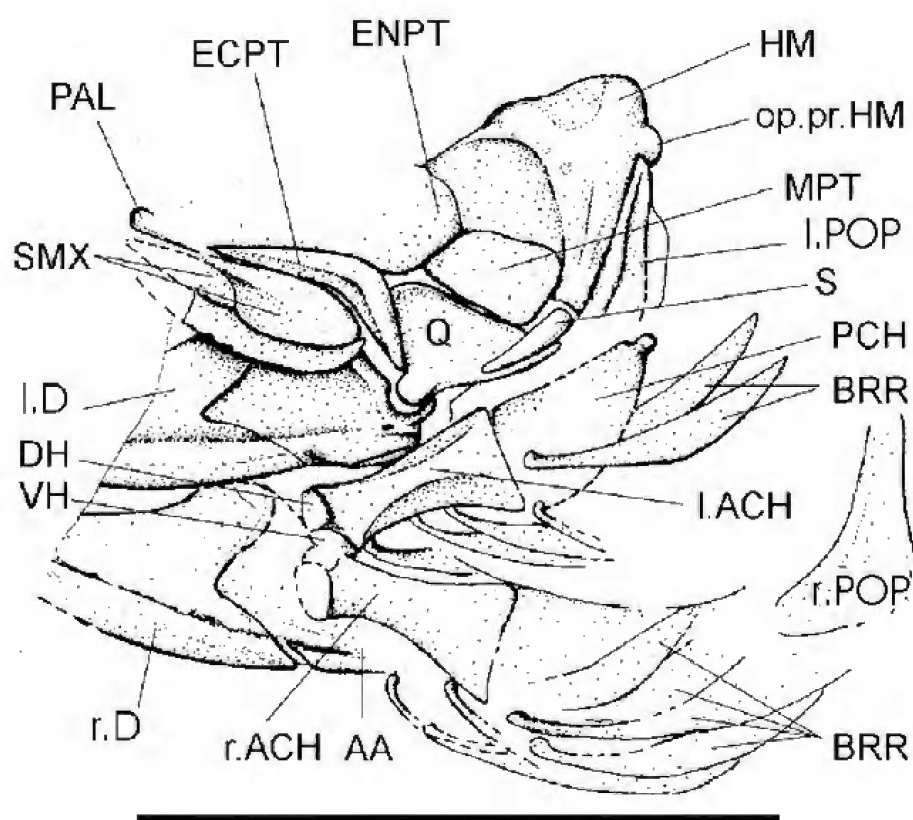

Fig.6- *Britoichthys marizalensis* gen. and sp.nov.: suspensorium, mandible, hyoidean series and opercular apparatus as preserved in the DGM 465-P. Scale bar = 0.5cm.

convex. The preopecular sensory canal pierces the bone near its anterior border and produces of about four to five atrophic tubules which do not reach the border of bone. The operculum (Figs.3-4, OP) is a large laminate bone, roughtly trapezoidal, with a rounded dorsal border and a straight ventral border. The operculum is of about five times deeper than the suboperculum. It is not as large and ovoid as in *Dastilbe* Jordan, 1910, but it is not as short as in *Clupavus brasiliensis* Santos, 1985. The suboperculum (Figs.3-4, SOP) is a large and falcate bone, with a short ascending process. The interoperculum (Figs.3-4, IOP) is a flimsy and long triangular bone often hidden in specimens by the ventral border of the preoperculum.

From the shoulder girdle the following elements have been identified: coracoid, scapula, cleithrum, supracleithrum, postcleithra, posttemporal and extrascapular.

The coracoid (Fig.3, CO) is a falcate and laminate bone. The anterior process is elongated and narrow and projects towards the ventral process of the cleithrum, but not reaching it. Posteriorly, it is large and expanded. The scapula (Fig.7A, SCA) is a reduced, massive and triangular bone placed on the posterodorsal corner of the coracoid. A reduced scapular foramen is present. It is not possible to determine the presence of a mesocoracoid arch. Due to the poorly preservation in all specimens, only imprints of short club-shaped radials (Fig.7A, rad) are observed. There are at least two (probably four) radials below the first ray. The lowermost radial is the largest. Considering the proximal dilation, the anteriormost lepidotrichum (Fig.7A, f.r.) is typically fused with a stout propterygium. It also appears to bear a dorsal splint. The position of the pectoral fin is relatively high on the flank but the base is horizontally positioned. The pectoral fin is composed of 15-16 segmented and distally branched fin-rays. There is no axilary scale.

The cleithrum (Figs.3, 7A, CL) is a roughly sigmoid bone. The bone is flimsy and its outer surface is smooth. The horizontal arm projects obliquely forwards slightly surpassing the limit of the anterior border of the suboperculum. It equals the length of horizontal arm of the preoperculum. The vertical arm is smaller and shows a reduced dorsal spine-like process. The lateral lamina is reduced through the lateral border of bone. There are two postcleithra behind the vertical arm. The upper one is a triangular and scaly bone whereas the lower one produces a spine-like process that extends ventrally and

medially behind the pectoral fin base. The supracleithrum (Fig.3, SCL) is a triangular and scaly bone lying oblique and laterally on the spine-like process of the cleithrum. The lateral line canal crosses obliquely the bone on its upper third. The post-temporal (Figs.3-4, PTM) is a large and drop-shaped bone in lateral view. The dorsal process is slightly arched and very prominent. The posterior portion of the bone is ovoid and laminate. It is pierced longitudinally by a short post-temporal branch of the sensory canal. The extrascapular (Fig.3, EXS) is a single large and triangular bone bearing the transverse supratemporal commissure.

The pelvic fin is similar to that of generalised salmonoids (see NORDEN, 1961). It is supported by an elongate and roughly L-shaped pelvic bone. Each pelvic bone is laminate, well ossified, and strengthened by a moderate longitudinal keel. The anterior end (pubic process) is spatulate and the posterior third bears lateral protuberances to support fin rays. The stout median process meets its fellow through a sinuous suture. The ischiadic process is acute and reduced. The fin is well developed and formed by ten rays. They are only segmented in the distal third and the end of each fin ray is branched. There is a comma-like pelvic splint, not fused with the reduced lateral process of pelvic bone.

Each vertebra is as high as long and lacks ornamentation. The anteriormost vertebrae bear simple epineurals apparently fused (Fig.7B, EPN) with the basis of neural arches. Epipleural ribs are absent. There are no autogenous vertebrae (except for that of ural centra). The articular processes are digitate and very reduced. The neural and hemal spines are very slender and long. The neural spines of the anteriormost abdominal vertebrae (Fig.7B, NS) are distally bifurcate, a similar condition verified in the salmonoid *Thymallus arcticus arcticus* (Pallas, 1776) (see NORDEN, 1961) and other euteleosts. Only vertebrae near the caudal complex bear well-developed neural and haemal lamina.

There are seven long and comma-like supraneurals in the predorsal region. The first is larger than other of the set. The pattern corresponds to the type 2 described by JOHNSON & PATTERSON (1996).

The dorsal fin originates at the level of fourteenth abdominal vertebra, at the mid-point between the posterior border of the skull and the origin of the caudal fin. This fin is composed of 13 rays, the first being accessory and the others long,

segmented and distally ramified rays. There are 12 pterygiophores supporting fin-rays. The anteriormost is the largest and falcate. It is ventrally notched while the others are reduced and slender.

The small anal fin is located at the midpoint between the origin of the pelvic and caudal fins, at the level of the thirteenth caudal vertebra. There is one accessory ray and ten distally branched. The endoskeleton support is composed of eight slender and thin proximal radials.

The caudal skeleton shows six autogenous hypurals, two epurals and three uroneurals. The first preural centrum possesses a reduced neural arch and spine, with anterior and posterior laminate outgrowth. The second preural centrum bears long neural and hemal spines edged with anterior laminate outgrowth. The first uroneural (Fig.8, UN 1) is slightly curved and does not extend forward beyond first preural centrum. Apparently it is fused with a dorsal outgrowth of first ural centrum. There is a shallow laminar outgrowth of the first uroneural (stegural). The second uroneural (Fig.8, UN 2) is straight and its proximal end finishes at the second ural centrum. The last uroneural (Fig.8, UN3) is shorter than other two. The first ural centrum supports the first and second autogenous hypurals. These are of equal size and are separated proximally by a large hypural foramen. The parhypural (Fig.8, PH) is fused with the centrum and shows no hypurapophysis. There are ten dorsal (eight are simple and two segmented) and at least 6 ventral procurrent rays (two largest ones are segmented). There are 10 dorsal principal rays above the diastema and 9 ventral principal rays below. No caudal scute is visible. There are two slender and slightly inclined epurals (Fig.8, EP). The first and second hypurals (Fig.8, H) are attached at the first ural centrum whereas the hypurals 3, 4, 5 and 6 are free from ural centra.

The scales are large and cycloid and do not present any crenulate or ornament border. No radii are visible. Only slight concentric circuli are observed on surface. The scales do not cover the median fins, cheek, and opercular series. The lateral line scales are pierced by a simple median tube.

DISCUSSION

Britoichthys gen.nov. as an euteleostean fish.

Britoichthys gen.nov. shows features found in many primitive teleostean groups (*e.g.*, ethmoideal commissural canal, lateral process of rostro
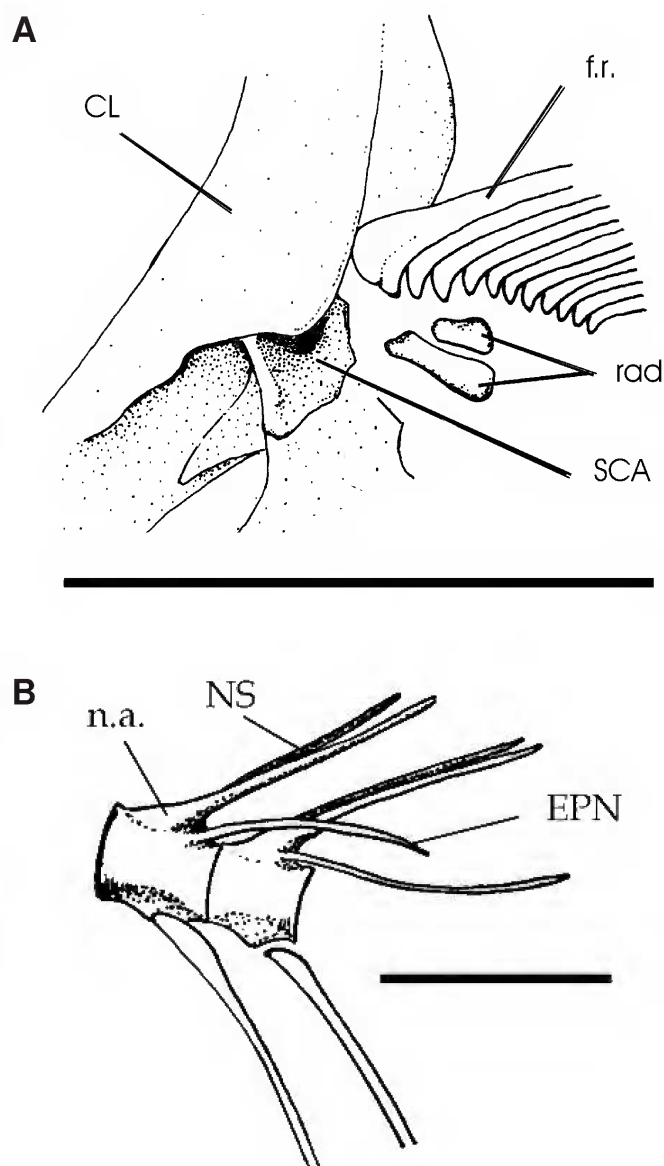

Fig.7- *Britoichthys marizalensis* gen. and sp.nov.: (A) pectoral girdle of DGM 466-P (scale bar = 0.2cm); (B) first abdominal vertebrae as preserved in 543-P, left lateral view (scale bar = 0.25cm).

dermethmoid, tripartite sensory canal pattern on skull roof, number and shape of infraorbitals, ural and preural centra not fused in the caudal endoskeleton). A delimited retroarticular in the corner of mandible and absence of rostral bones exclude the taxon of the Elopomorpha. The absence of ventral and dorsal scutes in the abdominal region and the caudal endoskeleton pattern exclude it from Clupeomorpha. *Britoichthys* gen.nov. also lacks apomorphies shared by osteoglossomorphs (*e.g.*, primary bite between dentigerous parasphenoid, palatine bones and tongue; 18 or fewer principal caudal fin rays; absence of supramaxilla; absence of supraorbital; see GUO-QING & WILSON, 1996). A reduced number of branchiostegal

rays and vertebrae, shape of premaxilla, and caudal endoskeleton are derived features verified in *Briotichthys* gen.nov. suggesting affinities with euteleostean fishes. But the current definition of Euteleostei is far from satisfactory (ARRATIA, 1997, 1999; FIELITZ, 2002; JOHNSON & PATTERSON, 1996; LAUDER & LIEM, 1983; PATTERSON & ROSEN, 1977; ROSEN, 1973).

BEGLE (1992) points out that Euteleostei is defined by the apomorphic presence of a toothed alveolar process under maxilla. *Britoichthys* gen.nov. exhibits this condition. However, skeletal apomorphies mainly from the hyobranchial apparatus proposed by him for inclusive clades are inaccessible in the specimens examined.

JOHNSON & PATTERSON (1996) listed three characters defining Euteleostei: (a) presence of stegural; (b) pattern 2 supraneurals, and (3) presence of caudal median cartilages. Concerning these features, *Britoichthys* gen.nov. exhibits two of them (*i.e.*, an anterior membranous outgrow to the first uroneural, herein interpreted as a stegural, and pattern 2 supraneurals).

ARRATIA (1997) defines Euteleostei as "clupeocephalans in which primitively the parhypural is laterally non-fused to its autocentrum, the neural spine of preural centrum 1 is absent; the neural arch is atrophic or absent; and a stegural is present". Regarding Arratia's definition, the caudal skeleton of *Britoichthys* is advanced in relation to basal euteleostean fishes. It obeys a general pattern of primitive argentinoid fishes where there are a spine of second preural centrum entirely developed, two epurals, tree uroneurals, six hypurals and large laminar outgrowth associated with neural arch of second preural and rudimentary first preural centra (*e.g.*, *Argentina silus* (Ascanius, 1775), see GOSLINE, 1960; PATTERSON 1970). BEGLE (1992) pointed out that one synapomorphy for the Argentinoidei is the presence of "large, leaf-like plates of bone (supraneural laminae) associated with rudimentary neural arches on PU1 and U1". *Britoichthys* gen.nov. exhibits this feature. However, it differs from the argentinoids primitively by the presence of separated ural and first preural centra. Unfortunately, other apomorphies defining the clade are also inaccessible [*e.g.*, greatly elongated distal basihyal with specialized dentition, see BEGLE (1992)].

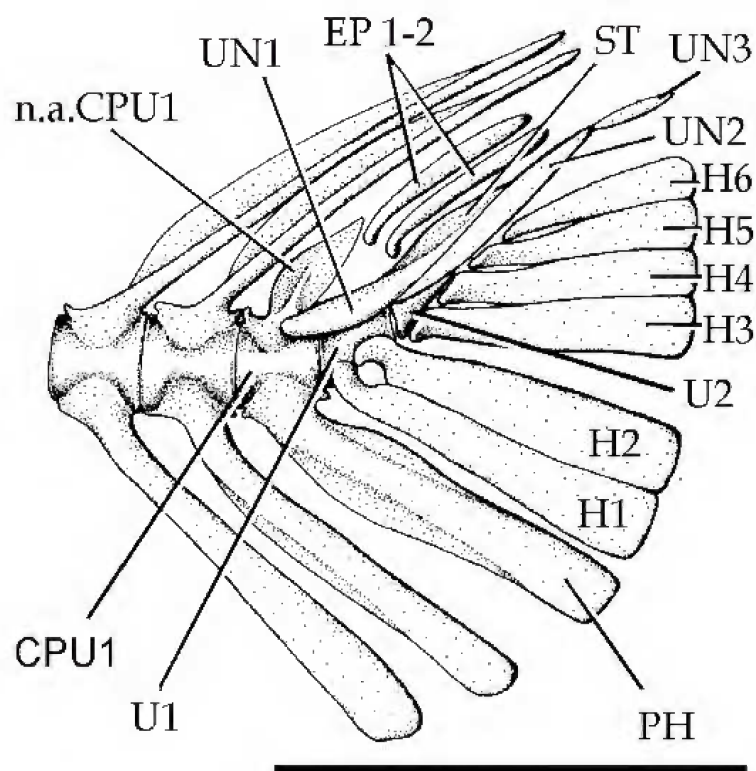PATTERSON & JOHNSON (1995) pointed out salmoniform fishes having epipleural and epineural

Fig.8- *Britoichthys marizalensis* gen. and sp.nov.: restoration of the caudal endoskeleton (based on DGM 466 and DGM 536-P). Scale bar = 1cm.

ribs without bifurcation and advanced members of group (osmeroid and salmonoid lineages) sharing the derived loss of the epipleural ribs. In this case, the absence of epipleural ribs and the presence of non-bifurcate epineurals in *Britoichthys* gen.nov. suggest affinities with salmonoids and osmeroids.

Despite of R. da Silva Santos having examined material herein studied, he has not included any description or mention in his PhD's Thesis (SANTOS, 1972) concerning fishes of the Marizal Formation. Seemingly, the material was sent to London, in the seventies, for occasion of his visit to American and European Institutions. According to Silva Santos (personal communication to the author) the material was presented to experts (Dr. D.E.Rosen and Dr. C.Patterson, from the American Museum of Natural History and British Museum of Natural History, respectively) that suggested, for attempt, the placement into euteleostean Galaxioidei *s.l.* group. But, while surveying literature on the systematics of Galaxioidei (*e.g.*, GOSLINE 1960; McDOWALL 1969, 1999; FINK & WEITZMAN 1982; BEGLE 1991, 1992; JOHNSON, 1992), morphological differences are verified, some of particular importance, that exclude the fish from tentative diagnoses of the clade (*e.g.*, presence of supramaxilla, well developed ectopterygoid, complete circumorbital series).

Britoichthys gen.nov. and certain Cretaceous basal euteleostean fishes

FIELITZ (2002), in the most recent review of lower euteleostean fishes, pointed out that only ten monotypic genera of Cretaceous teleosts belong to the group. The taxa are the following: *Avitosmerus canadensis* Fielitz, 2002, from the Turonian of Canada; *Barcarenichthys joneti* Gayet, 1989, from the Upper Cretaceous of Portugal; *Erichalcis arcta* Forey, 1975, from the Lower or Middle Albian of Canada; *Gaudryella gaudryi* (Pictet and Humbert, 1866), from *Gharbouria libanica* Gayet, 1988, from the Cenomanian of Lebanon; *Ginsbourgia (=Humbertia) operta* (Patterson, 1970); *Kermichthys dauini* (Arambourg, 1954), from the Cenomanian of Morocco and Sicily; *Manchurichthys uwatoikoi* Saito, 1936, from the Early Cretcaeous of China; *Paravinciguerria praecursor* Arambourg, 1954, from the Cenomanian of Morocco; and, *Stompooria rogersmithi* Anderson, 1998, from the Lower Maatrichthian of South Africa. Therefore, he considered that basal euteleosts are known from all continents except for Australia, South America, and Antarctica. His review omits remarks on the *status* of some Cretaceous teleosts putatively placed into

Euteleostei [*e.g.*, *Wenzichthys congolensis* (Arambourg & Schneegans, 1935), *Helgolandichthys schmidi* Taverne (1981), *Pyrenichthys jauzaci* (Gayet & Lepicard, 1985) and, particularly, *Santanichtys diasii* (Silva Santos, 1958), from the Albian of the Araripe Basin, North-eastern Brazil. This enigmatic taxon, known from few and poorly preserved specimens, was assigned to Clupeomorpha (SANTOS, 1991a, 1991b; FIGUEIREDO & GALLO, 2001), Euteleostei (MAISEY, 1991), or even considered a Clupeocephala *incertae sedis* (SANTOS, 1995). SANTOS (1995) also suggested putative affinities of the taxon with the Clupavidae, but considering this family placed into Clupeiformes *sensu* BERTIN & ARAMBOURG (1958). Although MAISEY (1991) has pointed out the presence of an anterior membranous flange on the first uroneural as evidence of inclusion of *Santanichthys* Silva Santos, 1995 in Euteleostei, its presence is uncertain. It is not exposed in his caudal restoration (MAISEY, 1991, non-numbered figure from p.273). Otherwise, the caudal restoration presented by Maisey for *Santanichthys*, is very similar to that of *Clupavichthys dufuri* Gayet, 1989, a probable ostariophysan clupavid fish from the Lower Cretaceous (Aptian) of Rio Benito, Western Africa (GAYET, 1989), suggesting close affinities between those taxa. At any event, the presence the second hypural fused with the first ural centrum and a very elongate second ural centrum easily separate *Santanichthys* from *Britoichthys* gen.nov. In addition, *Santanichthys* possesses dermal bones of the oral border (*i.e.*, dentary, premaxilla and maxilla) apparently toothless.

From the Fielitz's list, *Stompooria* Anderson, 1998 and *Paravinciguerria* Arambourg, 1954 lack stegural and *Kermichthys* possesses a pleurostyle similar to those found in ostariophysans differing therefore from *Britoichthys* gen.nov.

Avitosmerus canadensis, Wenzichthys congolensis, Gharbouria libanica, Helgolandichthys schmidi, Erichalcis arcta, Gaudryella gaudryi, Pyrenichthys jauzaci, Barcarenichthys joneti and *Ginsbourgia (=Humbertia) operta* are euteleostean fishes from Cretaceous from which relevant anatomical information is available. But most of apomorphic features proposed (see SANFORD, 1990; BEGLE, 1991, 1992; JOHNSON, 1992; JOHNSON & PATTERSON 1996) to define inclusive clades of Euteleostei, mainly of hyobranchial apparatus and soft tissues, are often not preserved in that fossil fishes. Their affinities are therefore uncertain. They are referred in current literature mainly as 'salmoniform' fishes so that a comparison with *Britoichthys* gen.nov. is furnished below. Other fishes assigned to 'Salmoniformes' based on

fragmentary or poorly described material (*e.g.*, *Manchurichthys* Chang & Liu, 1977, see CHANG & LIU, 1977) are omitted below.

Avitosmerus canadensis is known from the Cretaceous of the Great Bear Basin from Lac des Bois, Northwest Territories, Canada. This small fish shows a suprapreopercle, rostrodermethmoid and mesethmoid separated, besides a high grade of fusion of hypurals. These aspects are enough to distinguish it from *Britoichthys* gen.nov.

Wenzichthys congolensis is a well known pattersonellid fish from the Wealdean of Gabon (TAVERNE, 1975). It differs of *Britoichthys* gen.nov. mainly by the presence of a short and massive mesethmoid, absence of teeth on maxilla, absence of tripartite pattern for supraorbital sensory canal on frontal and fusion of preural 1 and ural 1 in the caudal skeleton.

Gharbouria libanica is a small fish described by GAYET (1988a) from Cenomanian of Lebanon. It is readily separated from *Britoichthys* gen.nov. mainly by the derived loss of teeth on dermal jaw, large orbit, shape and disposition of circumorbital bones.

Helgolandichthys schmidi from the Aptian of Helgoland (TAVERNE, 1981) differs from *Britoichthys* gen.nov. mainly by the structure of snout, absence of epiphyseal branch on supraorbital sensory canal, presence of a slender sympletic, and presence of a well developed stegural on caudal skeleton.

Erichalcis arcta from the Albian of Canada (FOREY, 1975) is distinguished from *Britoichthys* gen.nov. by the presence of mesethmoid and rostral bones separated on snout; absence of ethmoidean commissure, presence of pit-lines on parietal, presence of slender infraorbitals on circumorbital series, and single articular head on hyomandibula.

Gaudryella gaudryi from the Cretaceous (Cenomanian) of Lebanon (PATTERSON, 1970) differs of *Britoichthys* gen.nov. by various features. It has a long and slender ethmoid region, with rostral and mesethmoid separate, but without ethmoidean commissure or "pit-line". The parietal has a shallow transverse groove. The posterior margin of infraorbitals does not extend over the preoperculum. The premaxilla is small, curved and toothless, ending in a rudimentary ascending process and maxilla is toothless. There are few teeth on the dentary and higher number of branchiostegal rays (11) and vertebrae (43). The PU1 plus U1 centra, parhypural plus first and second hypurals, hypurals 3 and 4 are apomorphycally fused.

Pyrenichthys jauzaci described by GAYET & LEPICARD (1985) from the Maastrichtian of France is distinguished by the lower placement of pectoral fin on flank, higher number of branchiostegals (13) and presence of hypurostegy in the caudal endoskeleton.

Barcarenichthys joneti is a small fish described from the Cenomanian of Barcarena, Portugal (GAYET, 1988b), showing putative affinities with Osmeroidei. It is distinguished from *Britoichthys* gen.nov. by the weak dentition on dentary, reduced infraorbital bones, short supraorbital, slender hyomandibula, large orbit and outline of opercular bones, and caudal skeleton pattern (*e.g.*, three epurals, large stegural, first ural and preural centra fused).

Ginsbourgia (=*Humbertia*) *operta*, from Cenomanian of Lebanon (Patterson, 1970) shares various similarities with *Britoichthys* gen.nov., some of particular importance. The morphology of premaxilla, reduced and equal number of branchiostegal rays, reduced number of vertebrae suggest affinity. However, the current status of knowledge of the anatomy and affinities of fossil fishes previously assigned to the taxonomic "wasted-basket" Salmoniformes is so poor that any attempt to point close phylogenetic affinity is premature.

ACKNOWLEDGEMENTS

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